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The Winter Roosting and Awakening Behaviour of Captive Great Tits

By G. E. DUNNETT and R. A. HINDE
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1. Introduction

The roosting and awakening times of Great Tits (*Parus major*), measured with respect to sunset or sunrise, change throughout the winter months. In high latitudes the birds roost very much later, and awaken earlier, in mid-winter than they do in the autumn or spring. In England the changes in the roosting times are similar to those in the north but less marked: the changes in the awakening times are negligible. (see Kluijver, 1950, and other references given by Hinde, 1952). The length of the bird's working day is thus reduced less in mid-winter than is the solar day—the bird makes more effective use of the daylight at this season than in autumn or spring. In mid-winter food is probably scarce, and the nights are not only long but cold: it is thus likely that the tits need a long working day for feeding. The main purpose of this study was to compare the changes in the roosting and awakening times shown by wild birds with those of captive Great Tits given superabundant food, in order to obtain information on the causal mechanisms underlying the roosting behaviour.

2. Material

In October, 1951, four male Great Tits were placed in an aviary six feet cube. At first they were provided only with wooden shelter troughs and a rack containing fairly dense dead foliage for roosting: in late November four tit nesting-boxes were provided, and these were usually used thereafter. One of the birds died during December, and was replaced by another. The four original birds were marked with red (R), yellow (Y), green (G) and blue (B_1) rings. The new bird was marked with a blue (B_2) ring. Superabundant food was always present in the aviary. Observations were made on 37 mornings and 44 evenings scattered fairly evenly between October 16th and February 29th. The latitude of the place of observation was 52° 13′ N.

3. Behaviour before Roosting

Before nestboxes were supplied, the birds roosted amongst the foliage, pressed between a shelter trough and the wire netting, or in other similar sites. On November 27th one nesting box was introduced, and occupied on the first night by G. B. and Y also showed "interest" in the box, inspecting the hole after G had gone to roost inside. On the morning of November 28th three more boxes were hung up. R and G inspected the boxes immediately, and entered several times, sometimes staying in for some minutes at a time. That evening R, G and B. roosted in boxes: Y inspected a box several times, but roosted outside then, and also on November 30th and December 5th. On December 10th he also used a box. B_2, which was first introduced in late December, never used a box for roosting.

In general each bird used the same box on successive nights, but there were occasional changes. Sometimes a bird would inspect, and even enter, several different boxes just before roosting, but would usually settle down finally in its own.

Occasionally the birds fed right up to the time of roosting, but usually they sat around, often preening, for at least some minutes beforehand. There was one very marked difference from the behaviour of wild birds—these captive individuals often entered their roosting sites and emerged again several times before finally settling down. Often they would stay inside for several minutes, and then come out again. Such abortive entries were seen as long as 22 minutes before the final roosting time of the individual concerned. They were especially common in B_1, who would sometimes go in and out for several minutes continuously before roosting. Such behaviour is at least very rare in the field.

Aggressive behaviour over roosting sites was seen on a few evenings. Once, before the boxes were put up, two birds actually fought over a site in the foliage. On the other occasions one bird arrived at its box to find it already occupied, and perched below the entrance with wings raised and tail spread. Similar behaviour has been seen in the field. Even the dominant bird, Y, was apparently unable to dislodge a bird occupying his usual box once it was installed.

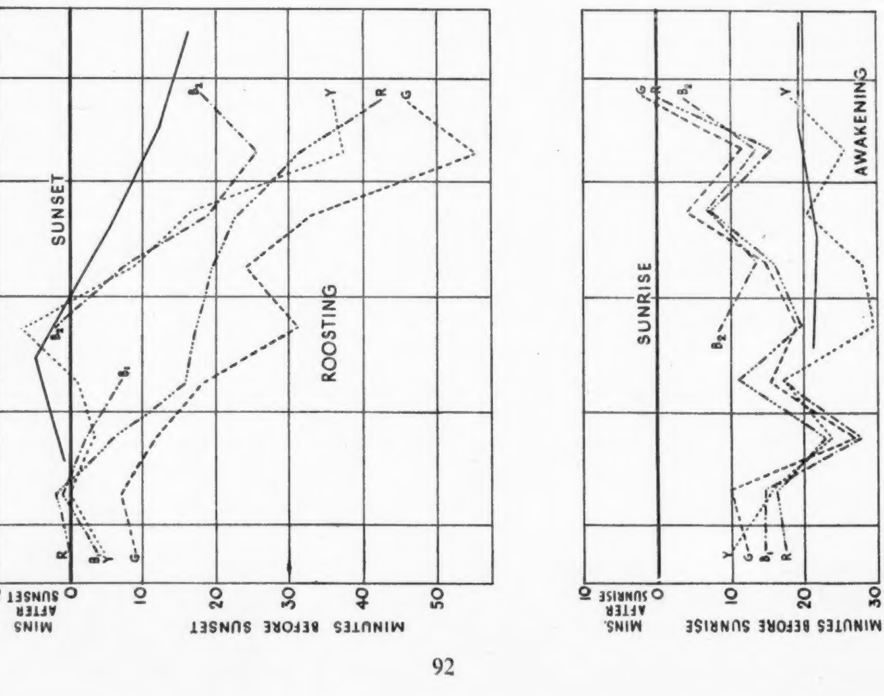

Fig. 1. Roosting and awakening times averaged by half months for each individual and plotted relative to sunset and sunrise.

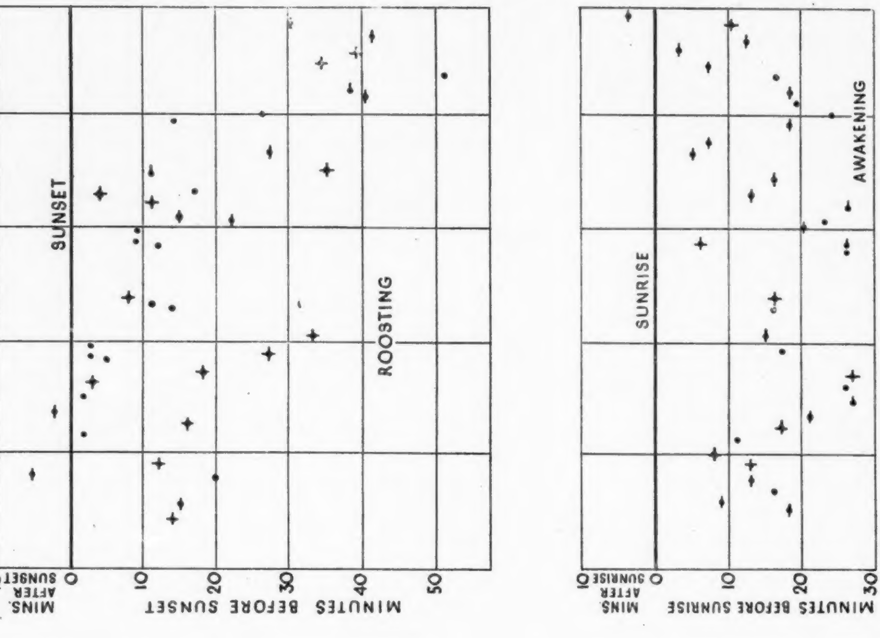

Fig. 2. Average roosting and awakening times of all individuals on each day that observations were made. For further explanation see text.

4. Behaviour on Awakening

On emerging from their boxes, the birds often sat around and preened a little, without feeding, for the first ten minutes or so. Aggressive behaviour was often very marked in the early morning, and Y often chased his subordinates vigorously. This aggressiveness was occasionally clearly related to food, but very often it occurred immediately after the subordinate had left its box, and food seemed not to be relevant. Y was the dominant bird throughout the winter. He was also the only one to show reproductive fighting towards strange Great Tits outside the aviary in the spring. He started to sing on the morning of January 11th, when the song consisted of an indefinite low warbling sub-song mixed with a few weak see-saw notes: the song became perfect by January 25th. None of the other individuals sang at all.

5. Roosting and Awakening Times

The records for each individual have been averaged for each half-month and plotted in Fig. 1. Owing to the considerable variation from night to night caused by fluctuations in the environmental factors, the averages must be treated with caution (see below and Fig. 2). The observations are sufficiently numerous, however, to make it certain that the trends shown are significant.

The two continuous lines in Fig. 1 indicate the roosting and awakening times of wild Great Tits in a wood near Oxford: the data are taken from Hinde (1952), and are in rough agreement with figures obtained by Kluijver (1950) in Holland.

(i) *Roosting Times.* It will be seen that :

(a) The captive birds roosted (significantly) earlier than the wild ones throughout the period of observation.

(b) All the captive birds went to roost earlier (relative to sunset) in spring than in mid-winter, as did the wild ones.

(c) This tendency towards an earlier roosting time appeared in two of the captive birds before mid-winter: both R and G roosted almost continuously earlier after the beginning of November. B_1, also, showed a similar tendency up to the time of its death. Y, on the other hand, roosted rather later in December than in October/November, but after mid-winter its roosting time became progressively earlier again.

(d) The individual differences in roosting times were considerable—the greatest difference on any one night being 52 minutes. It seemed that the individual variation on any one night was greater than that among wild birds, but four captive individuals are not a sufficient sample on which to base any definite conclusions. The birds usually went to roost in roughly the same order. G nearly always went very early, R was usually next, and B_2 and Y roosted at roughly the same time. But there was some variation from night to night.

(ii) *Dawn Emergence Times.*

(a) The birds awakened at a lower light intensity than that at which they roosted.

(b) The dawn emergence times (relative to sunrise) of all individuals were slightly earlier in late November and December than in October. After mid-winter one of the birds, Y, continued to emerge at approximately the same time for the rest of the observation period. In this respect its behaviour was similar to that of wild Great Tits. The other three tended to emerge successively later as the season advanced, until in late February they were emerging within a few minutes of sunrise. Since Y was the only individual to show any sexual behaviour, it seems possible that its behaviour was connected with its relatively high sex drive (see below).

(c) The emergence times of the captive birds were approximately the same as those of wild birds in mid-winter, but, with the exception of Y, became later as the season advanced.

(d) Individual differences were smaller than in the evening, but were still apparently greater than the individual differences seen in the field. The greatest difference on any one morning was 32 minutes, but this was exceptional. Much of the individual variation was due to the behaviour of Y—the other birds usually emerged in fairly rapid succession.

6. Effect of the Weather

In Fig. 2 are plotted the average roosting and awakening times of the four individuals for every occasion on which observations were made. A horizontal line on one side of the point indicates moderate cloud during the observations, and a horizontal line on both sides indicates heavy cloud. A vertical line through the point indicates rain, snow or fog. These conditions are, of course, associated with a reduction in the light intensity, and it is

Fig. 1. Roosting and awakening times averaged by half months for each individual and plotted relative to sunset and sunrise.

Fig. 2. Average roosting and awakening times of all individuals on each day that observations were made. For further explanation see text.

presumably for this reason that they are so often associated with earlier roosting times and later awakening times. A similar conclusion was reached by Kluijver. The correlation is, however, only a rough one, and there are many other relevant factors. For instance, on January 10th the birds roosted late in spite of heavy cloud, but this was probably because heavy rain had kept them under shelter and away from food most of the afternoon.

Kluijver (1950) found that the emergence of Great Tits in Holland was also delayed by strong wind and (slightly) by high temperature: weather conditions seemed to have little influence on the times of roosting. The data obtained in the present study were compared with temperatures and wind forces as registered at the Cambridge University Dept. of Geography three miles away, but no evidence of any effect of wind or temperature on either roosting or awakening times could be found. These data, however, are far less extensive than those of Kluijver.

7. Discussion

Seasonal changes in roosting and awakening times must be considered from two points of view—the biological advantages (if any) which they bring, and the causal mechanisms underlying them (Hinde, 1952).

For each species, in each locality, there is presumably an optimum length of the working day, determined in part by the time needed to discharge the various activities of life (feeding, sleeping, courting, etc.). The length of this optimum may be influenced by the susceptibility of birds to predators at different times of day—the dangers may be particularly great at dawn and dusk. The length of the optimum also varies with the latitude (in the winter Great Tits in the north have a longer day relative to the sun than in England), with the season (there seems to be a premium on early rising for males in the spring), and, of course, from species to species.

Each bird has a daily rhythm of activity which may be temporarily independent of external factors, and causes it to be active for a period near to the optimum. Thus Palmgren (reviewed 1949) has shown that if song birds are kept in continual light, they continue to roost and awaken at approximately the normal time for several days. This rhythm may be modified in a number of ways :—

(i) It is modified and kept in the correct relation to the solar day by certain environmental stimuli. Some of these (e.g., light intensity) have been discussed briefly above—more precise and detailed data are given by Kluijver (1950). The effect of these environmental stimuli changes from season to season—a Great Tit roosts much earlier (relative to the sun) on a dull day in March than on a similar day in December.

(ii) The diurnal rhythm of sleep is also influenced by other drives. Kluijver has shown this clearly in the case of the feeding drive—Great Tits kept short of food in winter roost later than when food is abundant: the dawn awakening time is apparently unaffected. This probably accounts for the rather earlier roosting times of the captive birds as compared with the wild ones, for the former had superabundant food. For the same reason, however, the influence of the feeding drive cannot be the direct cause of the seasonal changes in roosting times, for the changes were shown by the captive birds which always had superabundant food, and they began in some cases *before* the day-length available for feeding was at a minimum. (The changes may, of course, be of advantage to the birds in that they have a relatively longer time for feeding in mid-winter when they need it most).

The sex drive also seems to influence the roosting times, for males emerge earlier when the sex drive is at its peak. (Hinde, 1952). In the present study the only male to show any sexual behaviour continued to emerge at about the same time as wild birds during January and February, whereas those individuals whose sexual behaviour had been suppressed by the unnatural conditions of captivity emerged progressively later. (See also Franz, 1949).

(iii) Franz (1949) has suggested that the tendency for the awakening times to become later in high latitudes in early spring is due to a sort of inertia effect. He suggests that as the dawn is getting rapidly earlier, and the period of twilight shorter, the birds need some time to adjust their rhythm to that of the sun, and so wake later with respect to sunrise. It would be expected that such an effect would be smaller in temperate latitudes, where the changes in daylength are less rapid. This is in fact the case with wild Great Tits, which emerge at about the same time with respect to sunrise throughout the winter months in this country. As noted above, however, those captive individuals which did not show sexual behaviour did show a

tendency towards a later waking time even at the latitude of Cambridge. It seems that such a tendency may be normally present in wild birds, though countered by the increasing sex drive.

A similar inertia explanation could be applied to the changes in roosting time in early spring—as the season advances the birds roost progressively earlier with respect to sunset. This could be the result of a lowering of the threshold (Tinbergen, 1948)—with the long day the bird's roosting drive becomes so high that it retires even though the external stimuli for roosting (? falling light intensity ?) are well below the normal values at roosting time. The behaviour of three of the captive Great Tits, however, indicates that this is certainly not the whole story, for their roosting times became progressively earlier with respect to sunset *before* the winter solstice. Further experiments are needed to confirm this. In the field the latest roosting times usually occur in mid-winter (e.g., Franz, 1949; Kluijver, 1950; Hinde, 1952, for *P. major*), but in a study made by Odum (1941/2) on *P.a. atricapillus* the roosting times were later in October than in December, and thus followed a similar trend to that described for the three captive Great Tits.

It must thus be emphasized that although it is possible to get some understanding of some of the causal mechanisms underlying the roosting behaviour, many of the changes in the times are still quite obscure. The preceding discussion is intended primarily to indicate the way in which some of the problems may be tackled. Many further observations and experiments are needed.

Summary

1. Observations were made on the roosting and awakening behaviour of four captive Great Tits between October and February.
2. These captive birds, which had superabundant food, roosted earlier with respect to sunset than do wild Great Tits at the same time of year.
3. The captive Great Tits went to roost earlier, relative to sunset, in Spring than in mid-winter, as do wild ones. In two cases the tendency towards an earlier roosting time appeared before mid-winter.
4. The dominant bird emerged at about the same time, relative to sunrise, from December to February—as do wild ones. The other birds, whose sexual behaviour was suppressed by the unnatural conditions, awoke progressively later.
5. They tended to roost earlier and awaken later on dull days.
6. The causal basis of the changes in roosting and awakening times are discussed.

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Experimental Live Trapping of Rats, with Observations on their Behaviour

By HARRY V. THOMPSON
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Introduction

These experiments were done, during the course of other work, at the Bureau of Animal Population, Oxford, from 1941-1946. They formed part of The Bureau's war-time studies of rodent control, directed by Mr. C. S. Elton, and owe much to the work of Dr. D. H. Chitty. The help of the late R. M. Ranson and Miss M. N. Shorten is also gratefully acknowledged.

It is frequently necessary to obtain supplies of live rats for research or public health purposes. The commonest type of live trap is a wire box with a hinged door at one or both ends. The trap is set with the door(s) open and when a rat enters and attempts to take the bait from its holder, the movement of the latter causes the door(s) to fall and imprison the rat. Traps with a door at each end may be unbaited, rats being caught after releasing the trigger as they run through (Hovell, 1924). Normally only one rat at a time is caught in these traps, and we have observed that rats become shy of them.

The designing of rat traps seems to have engaged the attention of many people, and there is a large number of British and other patents of more or less intricate mechanisms for catching rats alive or dead. Most of the patentees have obviously no conception of the suspicion with which rats regard new objects, their traps are too complicated and consequently too expensive for general use. Native populations in various parts of the world have devised live traps for rats (Mérite, 1942).

There are three types of trap which can be employed to catch more than one rat at a time; the door can (1) be closed by a concealed observer (e.g. Hamilton, 1936), (2) close automatically when a certain weight of rats is inside, (3) allow successive rats to enter but not to leave. We have conducted experiments with these three types of trap, and also used them, in conjunction with census baiting, to calculate the density of certain populations.

The experiments described in this paper would have been taken further but for the ending of our field work. It is believed that a few more experiments would have led to a great improvement in the efficiency of the type (3) trap and it is hoped that other workers may be able to take over from the stage we reached. Much of this paper is concerned with presenting observations on the behaviour of the rat.

Types of Trap

(*a*) Hand-operated

It is a simple matter to devise a trap which can be closed by hand and in June, 1941, 23 rats were caught in such a trap (Fig. 1a) in four pulls, made during 4½ hours. The residual rats were watched 14-16 hours after the trapping and were very shy, some avoiding the trap altogether and only a few entering. The majority of those that approached it raked grains of wheat out through the wire, eventually clearing a space of about half an inch right round the inside of the trap next to the netting. It is unlikely that all these rats (at least ten) could have seen the capture of the 23 and so acquired trap shyness, and perhaps trapping had selected a proportion of the population that had been accustomed to feeding in the trap and left mainly those that had originally refused to enter it. However on another occasion there was an even more complete avoidance of this trap after a catch had been made, and it appears as though trap shyness may somehow spread throughout a population. The disadvantage of this trap is the large amount of time that has to be spent watching for the best opportunity to make a catch.

(*b*) Weight Release

There is one commercial trap (the "Pied Piper") that works on the principle of the floor giving way when a certain weight of rats is upon it, but the only extensive work that we have done is with a trap designed by Chitty

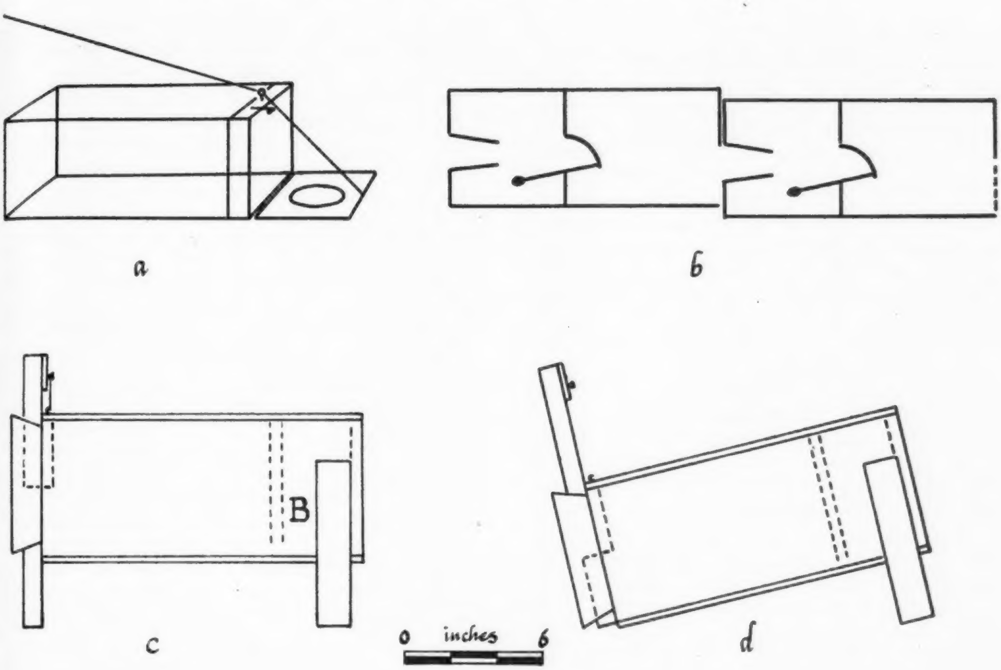

Fig 1.

(Fig. 1 c and d). It consisted of a box held three inches off the ground by one front and two back supports. Rats entered by a three-inch square hole in the front and took food from the bottom of a hopper made by dividing off a compartment along the back. The front support was a piece of wood six inches wide and taller than the trap, with a hole through it three inches above the ground and opposite the hole in the front of the box. From a screw in the back of this support near the top a loop of thin wire held up the front of the box. With sufficient rats inside the box, this loop broke, the front of the box fell and its entrance hole slid behind the lower three inches of the front support, which was held in place by vertical guides. Different gauges of wire were made into loops with different breaking points.

The trap was surplus baited with wheat continuously at an experimental rat colony, from August to November, 1941. On nine nights during this time the trap was set, and 106 rats were caught out of a large population. During the first eight catches (the largest of which was 28 animals, total wt. 5.4 Kg.) the trap was entered without any apparent shyness, but after the last catch a very definite trap shyness developed. This was illustrated by the results of baiting alternately inside the trap and on the ground beside it. The peak (maximum) takes of wheat were obtained on the following dates :

Nov. 1941:	5	9	14	15	19	20	22	24
Inside trap (g):	480	—	330	—	640	—	580	—
Beside trap (g.):	—	1025	—	1180	—	1440	—	1680

These takes represent approximately 19-23 rats feeding inside the trap and 41-67 feeding beside it. One possible explanation for the apparent lack of shyness during the first eight trappings is that rats were immigrating steadily throughout this period.

While this proved to be quite a good trap for catching some rats from a large population, it was no use on small populations, could not eliminate a population (because of trap shyness) and was too large for use in many sites.

(*c*) **Cumulative**

The Smeuse. Wild rabbits in a warren enclosed by wire netting will learn to go in and out through vertically hung doors (Southern, 1940) and it was thought that that principle could be used against rats. A wooden box was therefore made with an entrance and an exit tunnel, closed by slanting wire doors which allowed one-way traffic only. If the rats could be taught to go right through the trap, the securing of the exit door on a specific night would ensure their capture. The trap was put down at the experimental colony, and wheat in the entrance tunnel was eaten by the second day. Thereafter, up to the twelfth day, small amounts were eaten from just inside the door but the main pile of wheat in the centre of the box was untouched. It was evident that a rat (or rats) was pushing up the slanting door just sufficiently to get at a little wheat, but was unwilling to enter and allow the door to close behind it.

After this failure the rather heavy slanting wire doors were replaced by very light upright doors of perforated zinc, freely swinging upon an overhead rod. Before attaching these light doors, however, the rat population was surplus baited upon wheat for nine days in the doorless trap and took on the average 1 kg. wheat per day. When the doors were attached, there was no take of wheat at all for four days and the takes for the next eight were negligible.

The "Wonder." The name "Wonder" trap is used by Kunhardt & Chitre (1921) for the kind most widely used for catching rats in plague areas. Attention was now concentrated upon this type of mechanism as being the most likely means of catching rats for experimental purposes and also of eliminating an infestation completely. The trap was patented in England in 1883 by Henri Marty of Villefranche, France, and the design, practically unaltered, has been in frequent use ever since. The trap consists of two compartments made of metallic wire, the first being an entrance chamber nearly circular in end view and having a central turned in opening. It has a semi-circular partition fitted inside and arranged vertically across to form an interior gallery, while the rear end of the chamber is contracted and protrudes into the second compartment, being separated from it by a horizontal pivoted door opening downward and balanced by a weight just sufficient to keep it closed. The second compartment is merely a receptacle for the rats, which enter it from the first compartment, and at its rear is an opening through which trapped rats can be removed, the opening being closed by a door when the trap is in use. The inventor gives no directions for baiting the trap (a singular omission) but says " . . . When the trap constructed and arranged as described is properly baited, a rat or other animal attracted to it nibbles round until he comes to the simple entrance into which he passes without hestitation as no suspicious mechanism is visible. He then approaches the balanced door or platform intending to seize the bait, but the first movements of the balance suggesting a trap he starts back and endeavours to escape through the wire meshes which detain him, and raises himself in the gallery, climbing along the simple entrance to where, the partition being away, he would be able to see the opening through which he entered. At length, alarmed by the danger and convinced that there is no other exit, he returns to the balanced platform which sinks with his weight, dropping him into the second part of the trap and closing after him. Every effort to escape is then useless, and the bait remains to attract new captives." (There was no gallery in the type we tested.)

We are left to conclude that the bait was somewhere near the balanced platform (perhaps suspended above it), but in popular practice the bait is placed in the rear compartment, with the rear door closed. In all our Wonder trapping experiments the traps have been prebaited with the rear door open before any trapping has been attempted. In view of the shyness of rats towards almost all new objects, it seemed logical that trapping after pre-baiting would be more efficacious than without it. However, the absence of controlled experiments constitutes a gap in our knowledge that should be filled; especially as the behaviour of the rats on the night of trapping is different from that during prebaiting since they have to depress the treadle to get at the food.

Our work with the "Wonder" trap falls naturally into two sections. First, observations made at the experimental rat colony upon the behaviour of wild brown rats towards the original trap and its various modifications; and, second, its use in field tests. The most important aspect of the work is probably that dealing with rat behaviour, which sheds some light upon animal intelligence.

Some attempt is also made to assess the practical efficiency of "Wonder" trapping,

and to see what information it gives about the validity of our census technique. As an addendum to the second section, all brown rats (*Rattus norvegicus*, Berkenhout) caught in "Wonder" traps are grouped according to sex, weight and time of year when caught.

Watching the action of "Wonder" traps

(*a*) **Single traps**

The "Lobster Pot." The "lobster pot" entrance was designed to prevent rats from leaving the first compartment of the trap by the entrance hole and to encourage them to go over the treadle into the second compartment, where they would be caught. Although it was subsequently observed that tame white rats and young wild brown rats were sometimes baffled when trying to escape by the "lobster pot" entrance, adult wild rats had frequently been seen leaving the trap by the front entrance, and the necessity for having this first compartment seemed doubtful. An experimental "Wonder" trap was therefore made without a front compartment. The body of this trap was a large tin with an exit door at one end and a wire netting front, with a treadle similar to that in the "Wonder" trap in its centre. This experimental trap and a normal "Wonder" trap were placed together at the experimental colony.

General behaviour of the rats

Both traps were token baited with wheat, the rear doors being left open, and in a few days the rats were feeding freely from them. 50 g. wheat was placed in each compartment of the Wonder trap and 100 g. in the experimental Wonder trap at 4 p.m.* each day and, when the rats were fairly well conditioned, they were watched each evening for 20 mins. from 30 April to 7 May, 1943 (Table I). The number of rat visits to front and back of each trap was noted and the food was weighed after watching. Although the rats came out to eat within a

* All times given in this paper are G.M.T.

Table I. Number of Visits to Live Traps and Amount of Wheat Removed.
(F=feeding visits, N=non-feeding visits).

DATE	Experimental trap							Wonder trap							Totals			
	WHEAT																	
1943	Front		Back		Total		Take	Front		Back		Total		Take	Visits		Takes	g./ mouthful
	F	N	F	N	F	N	(g.)	F	N	F	N	F	N	(g.)	F	N	(g.)	
30 April	12	6	25	8	37	14	15	11	6	23	10	34	16	10	71	30	25	0·35
1 May	8	6	4	2	12	8	4	20	14	20	8	40	22	15	52	30	19	0·37
3 May	7	4	45	5	52	9	25	16	10	20	3	36	13	15	88	22	40	0·45
4 May	0	0	15	0				11	2	6	1							
	0	1	17	3				10	0	10	0							
	6	0	24	1	117	8	55	15	1	20	0	127	6	50	244	14	105	0·43
	10	2	15	1				17	1	38	1							
	2 : 1 RUSK																	
5 May	1	0	10	0				11	2	9	0							
	8	1	16	0				10	5	17	7							
	1	0	3	1	60	9	60	4	4	14	3	89	35	75	149	44	135	0·91
	3	5	18	2				8	5	16	9							
6 May	2	0	12	0				7	1	8	0							
	5	0	45	2				10	1	20	6							
	9	1	45	0	162	5	180	7	1	25	2	101	18	155	263	23	335	1·27
	4	0	40	2				8	1	16	6							
7 May	0	0	6	0				0	2	4	0							
	0	0	22	0				11	3	21	0							
	0	1	22	0	87	1	90	5	0	10	3	85	8	90	172	9	180	1·05
	0	0	37	0				5	0	29	0							

minute or two of the wheat being laid for them, their behaviour was very timorous and mercurial, especially during the first two days of watching. Any unusual sound was sufficient to send some of them scurrying to their holes and the most frequent cause of flight was the squeak emitted by one rat when trodden upon or pushed aside by another. By contrast some of the rats were very calm and one unusual individual remained in the front compartment of the Wonder trap for 19 min. and only moved when coughed at very loudly at the expiration of the watching period. Visits were of two kinds (*a*) hesitant, *non-feeding visits* by rats that came part or all of the way to a trap but did not take any food, (*b*) *feeding-visits* by rats that either ate on the spot or carried food away. A comparison between the relative number of feeding-visits and non-feeding visits to the traps upon the first four days of watching shows how the rats gradually lost some of their nervousness and the ratio of feeding to non-feeding visits rose from about 2 : 1 through 4 : 1 to 17 : 1.

They were first fed for four days on wheat and there was a similar number of visits to the two traps, in both cases more visits through the rear than front entrances. The number of visits per 5 min., on some days, gradually increased towards the end of the recording period but this effect was by no means so consistent as to appear significant (although there were always fewer visits during the first 5 min. than during any other similar period). During seven days' watching only two rats were seen to make one passage each from the front compartment of the Wonder trap to the rear one, via the treadle. No rat was seen to enter the experimental Wonder trap by the treadle, feeding visits to the front of that trap merely involving the scratching of wheat through the wire netting.

Behaviour with rusk

On the fifth day of watching, the food was changed to 2: 1 rusk (two parts water and one part biscuit meal) and there was a slight "new food reaction" in that the number of feeding-visits fell to 0.6 of that of the previous day while the number of non-feeding visits rose to three times that of the previous day. On the sixth day of watching the number of visits slightly exceeded that of the fourth, but fell by a third upon the seventh day. The total number of visits to both traps, in relation to the total food take during the watching periods, indicated that the average rat consumed or carried away on the average 0.4 g. wheat per visit. This implies that a rat of 220 g. body weight which consumes 24 g. wheat a day (Leslie, in the press) would have to make about 60 visits to the food supply in order to get his daily meal. When taking the rusk, however, the rats appeared to consume or transport a little more than 1 g. on the average. Since two thirds of the rusk was water, it appears that the rats would have to make the same or a slightly larger number of visits to obtain the same dry weight of food as they did in the case of wheat. Since some rats ate on the spot and some carried their food away, these estimates are necessarily approximate.

Trapping

Next the traps were baited with the rear doors closed, but on the first day (10th May) it was raining heavily throughout the watching period and there were only seven visits—three to the closed rear door of the Wonder trap and four to its front compartment only. The rear doors were therefore re-opened. On the following day the traps were again set and baited with wheat placed well at the rear of each. In 20 min. watching no rats were caught, although there were many feeding visits to the outsides of both traps (during which food was scratched from between the bars) and four feeding visits to the front compartment of the Wonder trap. The rats were watched for a little longer, and 5 min. later one entered the first compartment, stepped on to the treadle of the Wonder trap twice in succession, started back when it moved and ran out of the "lobster" entrance, stopped and came back. Two minutes afterwards the same rat stepped on the treadle three times in succession. It was still very timid when the treadle dipped beneath its weight but it bore the platform down, kept it down with its hind feet and, cautiously taking a mouthful of wheat, backed into the front compartment to eat it. After another minute the rat depressed the treadle for a fourth time, stepped off and was caught. For the next 12 min. the captive rat made no attempt to eat but spent its time trying to get out, biting at the bars and shaking them. The traps were left set overnight and on the following day there were five rats in the Wonder and none in the other trap.

For three days after this the rats were completely trap-shy during watching periods, i.e., the trapping had broken down the previous conditioning which brought them out to feed at 4 p.m.; but they ate small amounts of wheat

from the unset traps overnight. Later on the rats were again conditioned to feed at 4 p.m. in the traps but, instead of leaving the rear doors of the traps open, an attempt was made to accustom the rats to passing over the treadles. The treadles were canted down by hitching up the platform counter-weights; some free play being left so that the treadles would dip further when stepped upon. (Wheat was placed at the rear of the traps only). After some days, 20 min. watching showed that about half the feeding visits included a passage over a treadle. The following day (28th May) the traps were token baited as usual, the treadles released, and the rats' activities watched for 2½ hr. On thirteen occasions during the first 40 min. a rat passed over the Wonder trap treadle and was caught in the rear compartment; but four of these visits were made by one individual who escaped three times during the partial entry of other rats. There were in all thirteen of these partial entries or "treadle" visits to the rear compartment of the Wonder trap, i.e. a rat depressed the treadle and entered the rear compartment but did not remove all its weight from the treadle while feeding and was thus enabled to retreat back wards to the first compartment. While one rat was making a treadle visit rats already captured escaped by crawling over the visitor's back until only five remained. The rats in captivity sometimes went on feeding for a while but eventually made frenzied efforts to escape. These movements resulted in scattering of the wheat and more and more feeding visits were made by other rats to the outside of the trap, so that there were no further entries into the rear compartment after the first 40 min. Several small rats entered the first compartment of the Wonder trap and sat on the treadle, but too far back to depress it, while one rat entered the trap three times with the obvious intention of going into the rear compartment but shied off at seeing the treadle in the unfamiliar horizontal position.

There were no visits to the experimental trap during the first 35 min. but during the next 10 min. there were six "treadle" visits by a large rat which finally stepped off the platform and was caught. This rat threshed about and scattered the wheat from the trap.

The number of feeding visits fell off towards the end of the watching period. One small rat was seen to squeeze itself out of the front compartment of the Wonder trap through the bars. At 6.30 p.m.—as at 4.40 p.m.—there were five rats caught in the Wonder trap and one in the experimental trap. The traps were left set overnight but no more had been caught by the following morning.

Recapitulation and Discussion

While these experiments showed that the normal Wonder trap was much superior to the experimental trap without a front compartment, this superiority may have been due quite as much to the all-wire construction of the Wonder traps as to its front compartment. The practice of prebaiting the Wonder trap with the rear door open and the treadle in its normal position did not encourage rats to go from the front compartment to the rear via the treadle, which meant that—to be caught—the rats had to adopt a new behaviour pattern upon the night that the trap was set. To encourage the rats to go over the treadle, the rear door was closed during prebaiting and the treadle canted down so that they could pass freely to and fro over it. Although this familiarity with traversing the canted treadle resulted in rats crossing the horizontal treadle more readily on the night of trapping, the catch of rats was no greater than it had been (i.e., after prebaiting with the rear door open). It is of course difficult to compare these two trappings because one preceded the other by 17 days and some of the rats may still have been shy; also the first trapping had removed some of the rats from the population.

It was now thought possible that the advantage of the rats' better knowledge of the way into the second compartment might be offset by knowledge of the way out, which could quickly be applied during "treadle" visits, and another means of accustoming the rats to crossing the treadle was therefore tried. Two Wonder traps were wired together in series so that rats would enter the first one exactly as they would on the trapping night (Fig. 1b). During prebaiting they would gain further experience by operating the second treadle on their way to the open rear door of the second trap. Also by baiting in the first compartment of the second trap "treadle" visits would be impossible because of the extra distance.

Watching suggested that the number of rats finally caught was partly a matter of chance, depending on the amount, and time of onset, of panic among the captured rats; since the wheat that they scattered in their frenzied attempts to escape made it unnecessary for others to enter the trap. Also since bait could

be scratched out from between the bars, it seemed advisable to place it in a tray. It was also apparent that the Wonder trap was unlikely to catch a representative fraction of a breeding population because some small rats were unable to depress the treadle or, if caught, could squeeze through the bars.

(b) **Double Traps**

Original Type. Some months later, June, 1943, the rats in the experimental shed were surplus baited with wheat and took roughly 1 kg. per day.They were then given a surplus in an open "double Wonder" trap (two traps joined together) but the peak take was only 310 g. during the next 18 days. On closing the trap for 24 hours only three rats were caught. About a week later, 20 July, to encourage the rats to enter the trap, the treadle counterweights were hitched up—as in a previous experiment—prebait was placed in the third compartment and the rear door was left open after it had been found that some small rats could not escape from the trap even though the treadles were canted. The rats were thus forced to traverse a canted treadle to reach the food, whichever way they entered. When the rats were using the trap freely (14 days from the last trapping), the rear door was shut, the treadles were released, and the trap was baited as usual (28 July).

There was no activity for the first 10 min. of watching, then a rat entered the first compartment, passed over the first treadle into the second and third compartments, took a mouthful of wheat, returned to the second compartment, *depressed the treadle from inside the second compartment*, and escaped. This "expert" rat made four more visits to the trap during the 2 hr. watching, on one occasion staying to feed in the third compartment for 24 min. In escaping he either put his forefoot in from beneath the treadle and pulled it down, or else put it through the wires above and pushed the treadle down until the other forefoot could pull it. Three rats went right through the trap to the fourth compartment and were caught.

Several small rats and three of 100-140 g. body weight tried, but failed to depress the treadle, while two rats on entering the trap were visibly startled to find the treadle horizontal. Throughout the watching three old males occasionally walked across and around the stage, sniffed at the trap and peered into it but made no attempt to enter. On the following morning six rats were found in the fourth compartment of the trap.

Shortened Type. Since the double Wonder trap was very large and cumbersome, some further experiments were done in July, 1945, to see if it could not be reduced in size. Accordingly, a shortened double Wonder trap was made by cutting away the fronts and joining together the second compartments of two traps. During surplus baiting with wheat on the floor of the experimental shed 600-700 g. was taken, and a double Wonder trap and a shortened double Wonder trap were placed equidistant from the main entrance hole of the shed. There was a lag of 17 days before the rats became thoroughly prebaited to using the traps, perhaps because ordinary Wonder traps were being used by the occupier before and throughout the experiment. The rats could not be persuaded to come out to feed at 4 p.m. but appeared regularly at 7.30 p.m. in response to baiting with small quantities of wheat.

Watching the two unset traps in operation on three occasions showed that the shortened double trap was used much more than the double trap, but that the rats wasted a good deal of energy in trying to scratch wheat out of the sides of the first compartment, instead of entering the trap. There were also a large number of "treadle" visits. The rear doors of the traps were then closed and watching again showed the shortened trap to be used more. There were again many "treadle" visits, but 15 rats were found trapped by the following morning—11 in the shortened and 4 in the other trap (27 July, 1945). The fur over the rump of each rat was clipped with scissors and they were liberated. The positions of the traps were reversed and they were left open with token prebait wheat in each. Eight days later the closed traps were again watched and, as before, the majority of visits were to the shortened trap. After 18 min. watching a rat, weighing about 80 g. and with unclipped fur, passed over the first treadle of the shortened trap, ate a little wheat, and then passed over the second treadle. Finding the rear door of the trap shut, it operated both treadles in reverse and escaped through the entrance. The same rat returned 5 min. later and, after feeding in the first compartment, put its paw up from below the treadle, pulled it down and escaped. (This time it did not go over the second treadle). At least this rat and one other had discovered the trick of opening the treadle from the inside, for two rats fed

together in the first compartment of the shortened trap and escaped separately. The small number of "treadle" visits upon this occasion (four to the shortened and one to the double trap) perhaps indicates that rats which had previously made treadle visits had become the "experts"; indeed the small rat referred to earlier was seen to make three treadle visits and three expert escapes within five consecutive minutes. By the following morning (4 August) five rats had been caught in the shortened trap and two in the other; and of these seven, five had clipped fur. The rear doors of the traps were opened and the rats allowed to escape. They did not rush out immediately, but continued squealing and biting at the wires of the trap, and escaped only when they blundered across the open door. The positions of the traps were again interchanged and the open traps were token baited for the next nine days. When set, the double trap took two small rats, both with clipped fur; the shortened trap caught none (14 August). These rats were released and the population was surplus baited with wheat on the floor for the next three weeks. An initial take of 940 g. was followed by a gradual decrease to a steady 300-400 g.

Recapitulation and Discussion.

Certain old rats were observed to be too shy of the double Wonder trap to enter it and a population surplus baited upon wheat at a surface point took only one third as much when the wheat was placed inside the open trap. While this may have meant that all the rats were using the trap and eating a reduced amount of wheat, it seems more probable that a small proportion of the rats was obtaining much of its food in the form of wheat and that a larger proportion was avoiding the trap altogether or obtaining only a small fraction of its daily food from it. The catch on closing the rear door of the trap was so small (three rats) that the treadles were canted during the next period of prebaiting. This resulted in the capture of six rats when the trap was closed; but watching showed that some rats shied off completely on seeing the treadle horizontal and a number of others sat too far back to depress the treadle. The most important behaviour discovered was the ability of some rats to escape from the closed trap by operating the treadle in the reverse direction.

When testing together a double trap and a similar trap without the lobster-pot entrances it was found that the latter was much more freely used and caught over twice as many rats (11 to 4). When these rats were marked and released and the positions of the traps were reversed, more were again caught in the shortened trap (5 to 2), and five of these were marked. Watching showed that rats had learned how to operate the treadles in reverse. The captured rats were again released and the positions of the traps reversed; on closing them two were recaught, both in the double trap.

The reverse operation of the treadles without any forced learning is an example of problem solving for which there is no parallel in psychologists' experiments upon tame rats.

In July, 1943, the "expert" rat took wheat from the third compartment of the double trap and then immediately turned round and escaped over the first treadle. This rat might have learnt to operate the treadles during the prebaiting of the unset trap two weeks before, but it could only have crossed *canted* treadles for the preceding eight days. Since it turned round immediately after taking wheat and escaped by the way it entered, we may assume that the rat left the trap in this direction during those eight days; i.e., it never left the trap by the rear door.

Thus on the night of watching, it would have been unaware that this door was closed. The operation of the closed treadle by this rat was therefore either the immediate application of a lesson previously learned or an act of pure insight, based upon an appreciation of the mechanism of the trap.

It is worth noting that rats which went right through the trap to the fourth compartment, after feeding, were unable to escape, even though the "expert" made several escapes from the third compartment after their capture. This inability to imitate the "expert" is paralleled by the behaviour of white rats (Bruce, 1941), which were neither helped nor hindered in the mastery of a simple field situation by the presence of an already trained animal.

In July, 1945, the "expert" rat could not have been more than a few months old and was therefore unborn at the time of the earlier experiments. It may, of course, have had experience of normal Wonder traps (used by the occupier) and it is perhaps significant that it was not caught the first time that the traps were closed. The second time, this animal passed over both treadles of the shortened

double trap, as it may be presumed to have done during prebaiting. Upon finding the rear door shut, it immediately operated the treadle and escaped by the entrance. Although we may infer that this rat was in the habit of going right through the trap during prebaiting (i.e., over both treadles and out of the rear door) we may, from the behaviour of other rats, be virtually certain that before it learnt to do this so confidently it approached the trap in a more hesitant manner. It probably began by making "treadle" visits, and in so doing learnt to understand the treadle mechanism. This supposition is borne out by the fact that the same rat was seen to make "treadle" and complete visits in close succession. It seems probable that this rat also remembered that the rear door was shut for, when making a second visit 5 min. after the first, it did not cross the second treadle after feeding but immediately operated the first treadle.

It is interesting to note that of 15 rats caught (and marked) in the first trapping, five were recaught eight days later and two after a further 10 days. Since a night in a trap is clearly an uncomfortable experience for a rat, this suggests that the traps select the rats of less intelligence and/or less retentive memory, and that the majority—even of these selected rats—become shy of the traps after having suffered capture once or twice; or eventually learn the mechanism.

Since this shortened double trap seemed to be superior to the earlier double model, new traps were made following its design. The new traps had a longer first compartment (to discourage "treadle" visits) and each treadle was made to close against a rim which, it was hoped, would prevent "experts" from escaping. It was our intention to observe the reaction of the experimental rat colony towards these new traps, but the rat population had decreased by the time they were made. The traps were therefore tested elsewhere (pp. 106-8).

Field Experiments with "Wonder" Traps

(a) Single Traps

From time to time brown rats were caught in Wonder traps for use in laboratory experiments, but there are few data on population, size or proportion of rats caught. In the following cases (i) and (ii) are examples of very unsuccessful control, using these traps on small populations. The remaining tests were carried out upon much larger populations and show a fairly good return in number of rats trapped. However, even in these tests most of the rats remained untrapped. Estimates of the efficiency of the trapping are given on pp. 108-9. Experiments (iii-v) were done by Chitty, with Ranson's help in (v).

(i) *An allotment situated between two branches of the River Thames, with sheds for dogs, pigs, rabbits, hens, ducks and pigeons.* Not all the rats lived upon the allotment but some swam to and fro. Two protected poison points P3s and two Wonder traps (a large and a small one) were placed at different points on the allotment and baited with wheat. The rats were kept surplus baited in the P3s and token baited in the open traps, and at intervals the P3s were left empty and the traps were closed. At the beginning of the experiment the peak take was 295 g. (4 December, 1942) and after five trappings in two months the peak was 245 g. (2-4 February, 1943) seven rats havings been caught. The census immediately after trapping was usually much lower than could be accounted for by the small numbers caught, and may perhaps be attributed to some disturbance of the rats as a result of trapping. A week or two afterwards the take built up again to about the same as before. This recovery can scarcely be accounted for by the normal winter growth or breeding and there must have been a small but continual recruitment of new rats filling the niches left by those trapped (Table II).

(ii) *Butcher's shop.* Two Wonder traps were prebaited with the rear door open. Takes of wheat were 300-400 g., but only two adults and six recently weaned rats were caught when the traps were shut. None were caught when the traps were again shut, after further prebaiting.

(iii) *Experimental colony.* During July, 1942, the rat population was surplus baited with wheat in the shed. Four Wonder traps were put down during the census and were finally prebaited for two days and closed for four successive days, the night's catch being removed each morning. The number of rats caught each night (1-4 July) was 27, 4, 0, 4, showing the sharp fall in catch after the first night that is typical for the brown rat. Three rats were also caught in gin traps by the occupier on 2, 3 and 6 July. The average wheat consumption of the 35 live-trapped rats, as estimated from their weights (see Leslie, in the press) was 696 g., to which

Table II. Results of Three Months' Live-trapping on an Allotment

DATE (1942-3)		Take of wheat (g.)	Body wt. (g.) of trapped rats	Difference in take after trapping
4	Dec.	295	—	—
5	,,	—	♀160 ♀280	-110g.
6-7	,,	185 av.	—	-45
12	,,	250	—	—
15	,,	—	♀160	-115
16-17	,,	135 av.	—	-45
25-26	,,	205 v.	—	—
30	,,	—	♀205 ♂280	-13
31	,,	192	—	+75
6	Jan.	280	—	—
13	,,	—	♂245	-100
15	,,	180	—	-20
24-6	,,	260 av.	—	—
27	,,	—	♂325	-80
30	,,	180	—	-15
2-4	Feb.	245	—	

The last rat caught (27 Jan., 1943) was left in the trap another 24 hr. but no further rats were caught. The empty trap, rebaited and set, failed to catch any on 29 Jan.

should be added 67 g. for those taken in gin traps. This expected reduction in take of 763 g. compares favourably (Table III) with the observed average difference of 771 g. though there is obviously a large error in the mean difference between the takes. (The efficiency of live-trapping given in Table V is little affected by including the rats trapped in gins with those taken alive).

(iv) *Experimental colony*. After a census and prebaiting for a day in these same four traps they were set and caught 78 rats on 26th Aug., 1942. Each trap was crammed to capacity. The average wheat consumption of the 78 rats, estimated from their weights, was 1695 g., which is rather less than the observed drop of 1935 g. (Table III).

(v) *Experimental colony*. Six of the rats caught on 26th Aug. were marked and released on 30th Aug. After another census and prebaiting, the traps were set and caught 25 rats on 7th September including three marked rats. The average wheat consumption as estimated from their weights was 576 g.—on this occasion considerably more than the observed drop of 138 g. (Table III).

(b) **Double Trap**

(vi) *Cellars*. This experiment was carried out by Miss Shorten. Baiting in the cellars of a condemned block of property in the centre of Oxford, revealed a fairly large rat population that had access to the sewers through a dry open drain. A double Wonder trap was put down with the rear door open, and baited with wheat. Scattered wheat was removed to within 3 in. of the trap on the first day (21st August), some was taken from the back compartment on 22nd August, from the front compartment on 23rd August and small amounts from the inner compartments on 25-7th August. During the next week the take rose to 450 g. from the trap alone (31st August). Surface baiting was then recommenced and the takes from the trap dropped,

Table III. Takes of Wheat (g.) before and after Live-trapping in Oxford.
(*Rattus norvegicus*)

Experiment:	(iii)	(iv)	(v)	(vi)
Type of trap:	W	W	W	DW
Number of rats trapped:	35	78	25	20
Biomass (g.)	6115	15085	5050	3620
Av. body wt. (g.)	175	193	202	181
	June, 1942 22 2443 23 3670 24 2925 29 + 30 + July, 1942 1 ⊙ 2 ⊙ 3 ⊙ 4 ⊙ 5 — 6 — 7 2435 8 2125 9 2165	Aug., 1942 22 3850 23 3860 24 4080 25 + 26 ⊙ 27 2175 28 1850 29 1700 30 2060 31 2225	Sept., 1942 1 2005 2 2130 3 2145 4 + 5 + 6 + 7 ⊙ 8 1990 9 1870 10 1920 11 1965 12 1980	Sept., 1943 1 1370 2 1020 3 1110 4 1290 5 + 6 + 7 ⊙ 8 740 9 665 10 628 11 565 12 700
Av. last 3 days before trapping	3013	3930	2093	1140
Av. days 3-5 after trapping	2242	1995	1955	628
Total difference Observed	771	1935	138	512
Expected	763	1695	576	426
Av. difference per rat removed Observed	22·0	25·0	3·5	25·6
Expected	21·5	23·0	23·5	22·0
Expected (range)	19·5-24·0	20·5-25·5	21·0-26·5	20·0-24·5

\+ prebaiting in traps
⊙ trapping night

W = Wonder trap
DW = Double Wonder trap

while the total daily take rose to over double the highest take from the trap alone. This indicated that, when the trap was the sole baiting point, either a small fraction of the rat population was feeding freely on wheat or else a larger fraction was taking comparatively little per rat. In either case, there was evidently some dislike of entering the trap which is probably not explained by overcrowding. Four days of trap and surface baiting were followed by two days' baiting in the trap only. The rear door of the trap was then closed overnight, and 20 rats were found in it by the next morning, 7th September(*). Nineteen of the 20 were alive and were removed to a large outdoor cage and fed upon wheat and water. In the cellar takes of wheat (g.) were as follows:

Trap:	130	250–250	450	100	100	30	30		
	400–400*	–	–	–	–	–			
Surface	–	–	–	–	1270	920	1080	1260	–
points:	–	–	740	665	628	565	700		

The estimated average wheat requirements of the 20 rats was 426 g. per day (range 503-337 g.); which can be shown not to differ significantly from the observed difference between the mean takes of census wheat (512 g.). The observed daily average take by the 19 rats in the outdoor cage was 316–30.6 g. This figure is an average for eight days after the rats were caught; but because of trapping and the new environment they may not have been feeding to capacity. Their peak take on the seventh day was 435 g.

Tests of New Model

Several new models of the shortened double trap were made as described on pp. 106. The bait tray had sides $\frac{3}{4}$ in. high to avoid scattering of the bait, the first compartment was made longer to discourage "treadle" visits and the treadle closed against a rim to prevent "experts" from operating it in the reverse direction. To facilitate baiting there was a door in the side of the first compartment.

Six of these new double traps and four single Wonder traps were put down at seven infestations in the City of Westminster, London; two of the infestations being of *Rattus norvegicus* (brown rat) and five of *Rattus rattus* (black rat). A pre-trapping wheat census was carried out at surface points at five infestations and a post-trapping census at all seven. After 3-6 days prebaiting with rusk, the baited traps were closed for 1-5 successive days; the night's catch being removed each morning (Table IV).

The two Wonder traps placed at infestation No. 1 (brown rats) were entered on the first day of prebaiting, and all the rusk was eaten on this and the three succeeding days. The daily catch for the next three days was 17, 4, and 1: showing a rapid falling off from the initial catch. It was estimated that 40-50% of the rats

Table IV. Takes of Wheat (g.) before and after Live-trapping in London.

Experiment No.:	1	2	3	4	5	6	7
No. census points:	3	4	9	4	4	6	4
Type of trap:	W W	S S	S	W	S	W S	S
Date placed (Feb. 1946)	6 8	6 8	6	6	11	16 16	14
Species:	Rn	Rn	R2	R2	R2	R2	R2
No. of rats trapped:	22	1	0	13	0	1	0
Biomass (g.)	4570	300	—	1930	—	110	—
Av. body wt. (g.)	208	—	—	149	—	—	—
Feb. 1946							
3	—	—	730	170	—	—	—
4	—	—	765	180	—	—	—
5	460	1200	600	490	—	—	—
6	460	1760	600	530	—	—	—
7	700	3090	570	560	—	—	—
8	870	3860	395	490	70	—	—
9	890	2200	665	420	120	—	—
10	1160	3690	535	435	200	—	—
11	1240	2860	475	460	240	—	—
12	1275	0 0	0	½	120	—	—
13	1140	0 0	½	+	100	—	—
14	+ +	½ 0	½	+	120	—	—
15	+ +	+ ½	0	+	120	—	0
16	+ +	+ ½	½	⊙	0	—	½
17	+ +	+ ½	½	⊙	0	0 0	½
18	⊙	⊙	⊙	⊙	0	+ ½	½
19	⊙	⊙	⊙	⊙	0	+ ½	½
20	⊙	⊙	⊙	⊙	⊙	⊙	⊙
21	400	1600	435	420	100	340	620
22	550	0	690	460	150	590	750
23	725	0	545	385	110	965	650
24	650	1520	450	440	120	1090	505
25	545	1440	590	320	120	950	565
Av. last 3 days before trapping	1218	2917	558	438	113	—	—
Av. days 3-5 after trapping	640	?	528	382	117	1002	573
Total difference Observed	578	?	30	56	4	—	—
Expected	512	30	0	(253)	0	16·5	0
Av. difference per rat removed							
Observed	26·3	—	—	4	—	—	—
Expected	24·0	—	—	(20·0)	—	—	—
Range	21·5-27·0	—	—	(18·0-22·5)	—	—	—

Notes. Heavy type shows take of prebait from each trap; none (0), some take (½), complete take (+). Trappings nights : ⊙. The Wonder traps (W) were prebaited with about 50 g. of 1 :1 rusk in each compartment, and about 50 g. scattered outside the entrance to the first compartment. The shortened trap(s) were prebaited in the same way (except that a little rusk was placed on the leading treadle). During trapping the Wonder traps were baited with 200 g. rusk in the second compartment, and 50 g. in the first; the shortened traps were baited with 200 g. rusk in the first compartment and 50 g. on and just in front of the first treadle.

had been caught (Table V). With black rats the prebait in a single trap at infestation No. 4, was partly eaten on the first day and completely on the three days following. The daily catch for the next five days was 4, 2, 3, 2, 2: which is in marked contrast to the fall off in catch shown by the brown rat. The high post-trapping census figures for this infestation make it probable that rats were migrating into the premises during the trapping period (unless the wheat census formed only about one fifth of the rats' diet). It is thus difficult to calculate the efficiency of trapping, but it was probably of the order of 30-40%. The trap at infestation No. 6 showed one day's lag in entry of rats; all the rusk was eaten on the two days following and one rat was caught when the trap was shut for one day. In view of the 1 kg. take by the population, this was a very poor catch, but it is probable that only two days' takes of prebaiting was insufficient.

Six of the shortened double traps at five infestations (brown rats in one case and black in the others) caught one brown rat only. This was infestation No. 2, where there was a lag of two days during prebaiting, a partial take on the third day and complete takes of rusk on the next three days. This test was perhaps partly invalidated by disturbing events at these premises (p. 106); but during the trapping period rats were both seen and heard in the vicinity of the traps. In the four black rat infestations, the rats failed even to enter the first compartment of the trap. This is explained at infestation No. 5, by the fact that even the rusk outside the trap was uneaten for four days; but in the other cases the trap and not the bait was at fault.

It was clear from these tests that the new model was deficient in some particular, since the rats would not enter it. It is possible that the "lobster-pot" entrance, although found to be unnecessary in the watching experiments at Oxford, is an integral part of the trap. It is also possible that there is a greater period of lag before the double Wonder trap is used freely, and the amounts of prebait used were too small to provide a check upon this. The galvanised, brand new appearance of the traps may have scared the rats, but this is unlikely.

Efficiency of Trapping

Some attempt may be made to show the amount of control achieved in these experiments. The same general principles apply as to the estimates of control by poisoning. There are various ways of using the census data; all of which agree within general limits. The method used here is based on the difference between the average of the last three days in census 1 and that of the third to fifth days in census 2. There are, however, two special features of the trapping experiments (1) immigration may have occurred because of the restricted area affected by the traps (2) it is known how many rats were removed and what they weighed. This latter information can be used to provide further estimates of efficiency by assuming that the rats were feeding almost entirely on census wheat. (Chitty & Shorten, 1946; Thompson, 1948).

Suppose $\bar{x}_1$, $\bar{x}_2$ are the average takes in the first and second censuses and that E is the expected take of the animals removed calculated from body weights.* Then each ofthe following four calculations should agree in showing the fraction of the population removed.

$$\frac{\bar{x}_1 - \bar{x}_2}{\bar{x}_1} \;\ldots\ldots\; (1) \qquad \frac{E}{\bar{x}_1} \;\ldots\ldots\; (2)$$

$$\frac{\bar{x}_1 - \bar{x}_2}{\bar{x}_2 + E} \;\ldots\ldots\; (3) \qquad \frac{E}{\bar{x}_2 + E} \;\ldots\ldots\; (4)$$

Immigration during the postbait, by increasing $\bar{x}_2$, would lower each of these estimates except No. 2 (which would be unaffected); but No. 3 would be particularly biassed. Emigration or a greater freedom among the reduced population to take alternative foods would have the opposite effect. Now emigration seems unlikely nor were the traps so placed that the rats, in subsequently avoiding them also avoided the census sites. More alternative food may have been taken by some of the reduced population, especially at the experimental colony, but the error may not have been serious in the majority of these experiments as the reduction in the population was evidently rather small. Each of the estimates except No. 1 will be variously affected by the extent to which wheat census baits had supplanted other foods in the diet.

With sampling and other unknown errors only very approximate estimates can be expected (Table V); but quite obviously none of these experiments was successful as a method of control.

Since we have no figures for the intake of wheat according to body weight for *Rattus rattus*, calculations (2), (3) and (4) can be made

Table V. Estimates of the Efficiency of Control by Live-trapping

Experiment	Trap	Take of wheat (g.)		Diff. between censuses.	No. rats trapped.	Estimated wheat take (g.) of trapped rats	Catch % estimated by formulae.			
		Census 1 $\bar{x}_1$	Census 2 $\bar{x}_2$	$\bar{x}_1 - \bar{x}_2$		E	1	2	3	4
Oxford (iii)	Single	3013	2242	771	35	763	26	26	26	26
„ (iv)	„	3930	1995	1935	78	1695	49	43	52	46
„ (v)	„	2093	1955	138	25	576	7	28	5	23
London (1)	„	1218	640	578	22	512	47	42	50	44
„ (4)	„	438	382	56	13	253	13	58	9	40
Oxford (vi)	Double	1140	628	512	20	426	45	38	48	40

for No. 4 of the London infestations only if we assume that per kilo body weight the intake by this species is similar to that by *Rattus norvegicus*. The range of percentages in this case is very wide and, since there was certainly immigration at these premises, the extremes of success and failure are highly inaccurate.

Proportion of Wheat in the Diet

In the Oxford experiments (iii, iv and vi) and London No. 1 (pp. 105-6) where all four estimates of the efficiency of trapping are close together, we may conclude that in each case the brown rat populations were living almost entirely upon the surplus wheat provided as census bait. In the case of (v), there are theoretically two explanations for the discrepancy between the four estimates; either wheat formed only 24% of the rats' diet (difference in census averages as % of estimated consumption of trapped rats) or else immigration had occurred between the two censuses. The latter explanation is the more likely, as it would involve the immigration of only about 18 rats whereas, if the rats were eating only 24% wheat in their diet, this implies that about 400 rats were feeding at the census point, which is highly improbable. It is admittedly possible that the rats were not feeding entirely upon wheat during the pre-trapping census perhaps because of overcrowding but were taking more in their diet during the post-trapping census. A rise from 83 to 100% wheat diet would account for the small difference in census averages and this may have been combined with immigration.

* Expected wheat requirements may be calculated, using a graph constructed from the data of Leslie (in the press). In Tables 3 and 4 the total expected difference is obtained from the sum of the individual items (theoretically the more accurate procedure) but for all practical purposes an average obtained from average body weight may be used. This average and its range are given for comparison in the last two lines of the Tables.

Summary and Discussion

While the number of field tests is inadequate, it is probable that only a fraction of a rat population ever enters these traps and runs the risk of being caught when they are shut; the difference in take of surplus wheat from trap and surface points is an indication of this.

The traps are no use for small infestations, since they do not eradicate the whole population, and they only catch a fraction of the rats in a large infestation. Better control would probably be achieved if much larger numbers of traps could be employed. As a rule, however, live traps are expensive or bulky or both and at present their greatest use is to the research worker, e.g. Richter & Emlen (1945). These remarks apply mainly to the brown rat, upon which most work has been done, and more experiments should be carried out, especially on the black rat, using both Wonder and double Wonder traps. The black rat may not show the rapid fall off in catch on successive trapping nights that has been found to be such a typical feature of the brown rat, and thus a larger fraction of a population might be caught.

In testing the efficiency of live traps it would be very economical of time if the pre-trapping census could be omitted, and calculations made only from a post-trapping census and the estimated wheat consumption of the rats trapped. However this calculation (No. 4) leans heavily upon the supposition that the rats are feeding entirely (or almost entirely)

upon the census wheat, which is certainly not true under all conditions.

Composition of the catch of Brown Rats

Brown rats were caught between 18 August 1941, and 20 February, 1946, at ten localities, upon 51 occasions. Out of the total of 343 just over half (181) were females, contrary to the popular belief that males are predominantly caught in live traps (Hovell, 1924). Almost exactly half were rats between 100 and 300 g. in weight and about one fifth were greater than 300 g. weight. By an arbitrary division, rats over 300 g. were considered large and rats under 100 g. small (Table VI).

Table VI. Composition of the Catch of Brown Rats in Live Traps.

S=small (<100 g.); M=medium (100-300 g.); L=large (>300 g.).

Months :	Winter (Dec.-Feb.)			Spring (March-May)			Summer (June-Aug.)			Autumn (Sept.-Nov.)			All Seasons			Total No.	%
Size:	S	M	L	S	M	L	S	M	L	S	M	L	S	M	L		
Males	1	15	13	4	8	1	32	31	13	8	27	9	45	81	36	162	47
Females	1	18	11	11	10	3	34	38	11	10	27	7	56	93	32	181	53
Totals	2	33	24	15	18	4	66	69	24	18	54	16	101	174	68	343	
Totals (%)	3	56	41	40	49	11	41	43	15	20	61	18	29	51	20		

Very few small rats were caught in winter, larger numbers in the spring and summer (about 40% of the catch), fewer again in the autumn. As would be expected, catches were greatest in the breeding season. Medium-sized rats formed the bulk of the catch all the year round. Large rats formed about 40% of the catch in winter, were fairly scarce in spring and summer, and increased in numbers in the autumn.

Although the numbers are too small to warrant sweeping generalizations, it is fairly clear that approximately equal numbers of males and females were caught in each size group, by totals and by seasons.

Summary

(1). Large numbers of brown rats can be taken in certain kinds of live traps but the remaining population may develop trap-shyness.

(2). The behaviour towards the wire "Wonder" trap and its treadle mechanism was watched at the experimental colony of wild rats. Even after several days' prebaiting the majority were shy, so that it seemed unlikely that good catches could be obtained on newly placed traps.

(3). When the back door or the treadle was wired open the rats had to learn a new method of entry on the trapping night and many shied off. Others kept their hind quarters on the treadle when taking the bait and some of those already captured got out.

(4). These difficulties were overcome by incorporating a second treadle and another compartment so that the rats went through identical procedures during prebaiting and trapping except for their inability to leave through the rear door. Unfortunately certain rats learnt how to work the treadle mechanisms in reverse.

(5). Field experience suggests that live traps of existing designs do not give efficient control, though catches of 40-50% of the population were achieved at two localities (other than the experimental colony). Any increase in efficiency probably demands rather large numbers of traps and an improved design (towards which a start has been made).

(6). The rats caught were fairly representative samples except in the lightest weight groups.

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APPENDIX

Habitat Notes on Infestations in London

1. There was a fairly large number of brown rats in the ground floor premises of a horse meat butcher's shop and in the basement beneath. The rats came from a sewer in the basement through holes in the concrete surrounding the inspection cover.

2. This heavy infestation of brown rats was in the ground floor premises of a butcher's shop and in the unused and dilapidated cellars beneath. Rats were seen in the shop occasionally but clearly lived in the walls, loose earth and rubbish of the cellar vault. A satisfactory census was done before trapping; but liver was left in the shop on the second night after trapping and the rats ate two or three pounds of this and no wheat. On the third night there was again no take of wheat, and although no meat was said to have been left in the shop, a cat was reported to have been seen mounting guard over the holes in the cellar. Takes of wheat on the other three nights were much lower than those of the first census, although one rat only had been trapped.

3. A moderate black rat infestation was living in the undisturbed cellars beneath a Chinese restaurant. There were piles of potatoes and onions on the floor but these were very little eaten by the rats.

4. There was a moderate number of black rats in the wine cellar and main cellar of a club. They were living in holes in the floor, walls and ceiling.

5. This dairy and grocer's shop had a small black rat infestation in the basement store room, where there was a great variety of food: fats, fresh fruit, dried fruit and cereals. In view of the available foodstuffs the census may have been incomplete.

6. A large black rat infestation in the cellars of a shoe shop. This infestation was not found early enough for a census to be done before trapping.

7. Large numbers of black rats were living in the walls and ceiling space of the basement kitchen of a milk bar.

Flocks and Herds at Free Range

By SIR R. GEORGE STAPLEDON

The methods and aims I propose briefly to discuss are different from but complementary to those dealt with in the papers read at the Conference.* In the trials to which I shall refer we have obtained most of our critical evidence rather from a close and oft-repeated examination of the herbages to which the animals have had access than from a systematic and long-continued watching of the animals themselves. This regular recording of differential defoliation by the animals as a means of estimating their preferences for various plants and herbages, and the intensity with which these latter are grazed is however like "watching" a matter of sustained observation. It is a method which if carefully employed over long periods throws a great deal of light on animal behaviour. The method gains much in value if supported by some sensible scheme of watching; and my chief aim here will be to draw certain conclusions which point to the usefulness of even a limited plan of watching and to make suggestions for the further development of the rather rough and ready plant-animal technique which we have employed.

The Trials

Brief particulars will here suffice. The first trial (on the farm of Lt.-Colonel Houghton-Brown at Lower Pertwood, Hindon) was conducted on a paddock of 200 acres. Fifty of these had been ploughed out of Down and cropped and were sown into eight mixtures under Barley in 1948. The plots were six acres each, and as well as a complex mixture including herbs; Meadow Fescue, Cocksfoot, Timothy and Perennial Rye Grass were sown in separate plots each with S100 White Clover. In the case of Cocksfoot, Timothy and Rye Grass there were separate plots respectively for mixed Aberystwyth strains and Danish (Cocksfoot), American (Timothy) and Irish (Rye Grass). A herb strip of two acres was also sown. The paddock is used for wintering North Devon Steers (about two years old) from 1st November till the middle of April. A smaller number of steers are kept on till August, and at the end of April or early in May a large flock of ewes and lambs are introduced. The paddock is usually completely rested during August, September and October. Here then we are able to study the behaviour of both cattle and sheep in large numbers and on a paddock offering 150 acres in natural Down Sward together with 50 acres in contrasting ley herbages.

The second trial (on the farm of Mr. J. F. H. Thomas at Stoke Farm, Broadchalk) was of the same type as the first, but it consisted only of sown ley herbages. Here the plots were five in number, each of 15 acres, and included a complex mixture (with herbs) and separate plots sown respectively with mixed strains of Perennial Rye Grass, Cocksfoot, Timothy and Meadow Fescue each with White Clover S100. There was no herb strip. These plots were sown under spring oats in 1948. Here the grazing was to all intents and purposes continuous throughout the year, and the aim was to maintain continuity of stocking at low density, so that the swards were never differentially punished to the same extent as they frequently were at Lower Pertwood. At this centre the stocking was wholly with ewes and lambs and with young stock destined for milk production.

The two centres afford interesting contrasts alike in the type of stock grazed, the management, the size of plot in relation to the head of stock, and in respect of association with or without a large area in natural Down sward. At both centres grazing was started in November, 1948, so that we have had over two years in which to accumulate evidence.

Method of Watching

With only myself (whose working day is now a short one) and my assistant, Miss Dorothy Wheeler (who has a great deal on her hands) available, any plan of continuous watching over prolonged periods was out of the question. Our aim was to concentrate on the first trial and to get onto the field as often as possible and at each visit to note the particular areas or plots over which the animals were distributed. At crucial times and at crucial dates the two of us would intensively watch for periods of up to a couple of hours or so; while (since we had other trials near at hand) we were frequently on the field (or near enough to make observations) several times during a day. We were greatly assisted in obtaining information by Colonel Houghton-Brown himself and by his foreman and shepherd. Taking it all together

* Symposium on Grazing Behaviour, held at The Zoological Society, London, on 13th January, 1951.

we have a very fair picture of how the animals have disposed of themselves throughout the whole period except for the hours of darkness, while at certain periods Miss Wheeler or I have been on the paddock almost daily for a matter of weeks at a time. Neither Miss Wheeler nor myself have been able to do much watching at Stoke Farm, and have had to content ourselves with periodic visits, but Mr. Thomas has provided us with a great deal of accurate information from his own keen observations.

The General Behaviour of the Stock

The Down sward at Pertwood was undulating and afforded shelter, on one aspect or another, at all times. The drinking trough was on the Down. The sown plots were relatively more generally exposed. Neither the cattle nor the sheep at any time (stormy or fine) camped on the ley swards. It was noted when watching animals on the lands of the Cahn Hill Improvement Scheme some years ago that both cattle and sheep always camped on virgin vegetation and not on the sown swards and there these latter were distributed on all aspects. It would appear that the animals prefer a dense and relatively matted vegetation to camp upon. Taking the sheep grazing period as a whole, the ewes and lambs spent very decidedly more grazing time on the ley swards than on the Down, indeed during periods of ample grass on these swards the amount of actual grazing time spent on the down would frequently have been no more than about 15 per cent. During each period of 24 hours the sheep spent some proportion of their time on the Down and generally (but by no means always) spent a certain amount of time (if only a little in certain cases) on each of the plots. The cattle spent relatively a great deal more time on the Down than did the sheep and sometimes for a run of a few days together they did not visit the swards. During the time when sheep and cattle were on the paddock together, the former did not permit of the growth of much sward grass for the cattle. Even so however but few days passed when the cattle did not spend an appreciable to a very considerable proportion of their grazing-time on the swards. The steers were bought-in, the ewes were a home bred flock. The steers showed a decided tendency to keep in separate parties. The ewes and lambs when first turned into the paddock would spend a couple or so exploratory days more or less as a mob together and then would settle down on the most palatable plots (the Timothy) where they would spend nearly all of their grazing time for a couple of days. There after the flock would become more dispersed, and would soon settle down to a more or less regular routine. They would fairly rapidly graze their way from their camping place on the Down to the higher end of the plots and then graze right across the plots, remaining longest on those that they "liked most"—most usually they would return over the plots, but would not always go the whole way back. Having arrived at their farthest point they would usually go out on to the Down, and this might not be until nearly dusk. The pattern was always interesting; sometimes there would be a spread practically across all the plots, but almost invariably there would be at least a 50 per cent density on the plots of a particular species. In hot weather, during the heat of the day, the sheep would spend all their time under and near the shade of thorn bushes on the Down. At Stoke Farm (where there was no Down and where the plots were larger in relation to stock numbers) the sheep practically monopolised the Timothy and Meadow Fescue plots, but each day they would go to the other end of the field and spend some hours on the mixture (and herb containing) plot.

The cattle like the sheep settled down to a fairly regular routine. During such time as there was ample grass on the ley swards the cattle would nibble their way up to the swards much more rapidly than the sheep and they would spend the whole of their first grazing period on the particular plot or plots which gave them the greatest quantity of easily taken lush grass. Then they would tend to wander off on to the Down; perhaps later in the afternoon they would make quite a long treck (not grazing the while) to a plot of their fancy. On several occasions I have watched a large party march up to the Timothy plots, graze slowly across them and back again and then solemnly return to the Down.

Seasonal Behaviour and Selectivity

At Pertwood the grazing season started on November 1st after the paddock had been rested for three months. At that date the Cocksfoot had made such massive growth

that it was totally unpalatable. All the other plots were highly palatable and at this time there was also plenty of green and palatable herbage on the Down. Almost immediately however the cattle showed a partiality for the ley swards and right on till well into December they took their first and heaviest meal off the mixture and rye grass plots, and also grazed the Meadow Fescue and Timothy as long as these lasted, but they almost completely neg-neglected the Cocksfoot. Later when the ley herbage became very scant, none the less they were on the rye grass and mixture plots every day but had to depend increasingly on the Down for bulk of feed, supplemented by Barley straw. The first grass to start really growing in the Spring was Cocksfoot (largely as a result of not (to all intents and purposes) having been grazed since August 1st, and by early March a wealth of green leaves were coming up through the mass of winter burned and half rotted material. From March 14th until the middle of April the Cocksfoot plots were giving more feed and held a far greater concentration of cattle grazing hours than any other similar sized area on the whole paddock. From that date until the Meadow Fescue and the Perennial Rye Grass began to come into head, all the plots were palatable.

The Timothy and Meadow Fescue were of outstanding palatability and by May 13th (dry 1939) there was hardly an accessible leaf to be grazed on the Timothy plots and the sheep (which had been on the paddock for a fortnight) perforce neglected these plots. It rained on the following days and the Timothy picked up very quickly and on the 16th all the sheep were again on the Timothy. At this time the cattle when coming to the plots concentrated on the Rye Grass which had not been grazed as hard by the sheep as the other plots. By early June the Meadow Fescue and the Rye Grass plots were coming into head and both series of plots were largely neglected by cattle and sheep alike. It was noted however that the lambs in particular had a partiality for the immature Meadow Fescue heads.

During June of this dry year Cocksfoot was providing more green leaf than any other plot and it was well grazed while the Timothy was kept grazed to the bone. The mixture plot (with far less Rye Grass and Meadow Fescue heads than on the pure plots of these species) was well grazed all through the period and right on till the end of July. The Cocksfoot however, continued most productive and relatively palatable till the end of the grazing period.

In wet 1950 the Rye Grass plots did not head as excessively as in 1949 and were relatively much better grazed during June and July while in this wet year the Cocksfoot tended to grow out of its palatable stage during these months. What was left of the Timothy was as palatable as ever, as was the Meadow Fescue except when in head.

It is of interest to note that at all stages the leaves of chicory were well grazed by both cattle and sheep and that during the dry spells of 1939 the chicory was subject to particularly heavy differential defoliation.

If we take the evidence of both centres and of both years together and the average for the whole grazing period we can place the animals' preferences as under:

(1) Timothy
(2) Meadow Fescue
(3) Mixture with Herbs
(4) }
(5) } Rye Grass: Cocksfoot

In dry 1949 both the sheep and cattle preferred Cocksfoot to Rye Grass, in wet 1950 they both preferred Rye Grass to Cocksfoot. If anything, sheep showed even a greater relative preference for Meadow Fescue than did cattle. The white clover growing with the grasses was well grazed at all times.

A point of some interest is the time spent by the cattle, particularly during the winter period, grazing very short herbage—both on the plots and on selected patches on the Down—herbage of the type which would have afforded very little bulk per unit of time spent grazing. The cattle obtained bulk on the coarser (and largely winter burned) vegetation and a better concentration of nutrients on the more difficultly won short (and green) herbage. Critical dawn to dusk watching of individual animals supported by sample taking would be of great value with reference to this essentially nutritional behaviour.

Conclusion

This brief account of the trend of results given by a combination of observations made on the swards and on the animals I feel justifies my claim that here we have the makings of a technique that could be used to very good purpose. Accurate scatter charts of the animals' disposition over the various swards through the

hours of daylight at regular intervals would be exceedingly revealing. Revealing too would be separate charts for animals which were "good" and "bad" doers, and for those which were "normal" and "abnormal" in their social habits. Our watching has indicated that there are wide differences in the behaviour of animals in these and other respects. My own view is that flock and herd watching of the type here described would well repay the time and energy of a team of workers and should precede schemes of watching of a more intimate character on individual animals. Herd watching under conditions of great freedom of action and choice can be relied upon to indicate the more urgent of the problems which the animals set us for solution.

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Grazing Habits and Trace Elements

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The few remarks which I wish to make are from my own experiences in our investigations as to the best means of combating cobalt deficiency in sheep. As a result of many field experiments we had discovered that on arable grassland, under the conditions of husbandry common in Scotland, the best method of feeding cobalt to sheep was to topdress the first year grass with 2 lb. of cobalt sulphate per acre. The cobalt dressing was so small that superphosphates were added as a filler to allow of an ordinary manure spreader being used. The dressing of 2 lb. cobalt sulphate per acre on first year grass made the herbage cobalt adequate for at least 3 or 4 years, thereby ensuring that one such topdressing only was necessary per rotation. Being assured of this from many practical tests we suggested to farmers that perhaps topdressing half a field would be sufficient as we presumed the sheep would graze the cobalt dressed pasture often enough to secure the amount of cobalt necessary for health. One or two farmers and shepherds who adopted this scheme soon drew our attention to a peculiar behaviour in the flocks, namely that they spent practically the whole day on the cobalt dressed half of the field. Soon it was evident that the cobalt dressed half of the field was much more eaten down than the half which had received the same dressing of superphosphates but no cobalt. The effect became very obvious and a source of worry to the farmers concerned. The effect, once started, soon became aggravated since the sheep naturally preferred the younger grass on the well eaten area to the longer stemmed grass of the not-so-well eaten area. This phenomenon excited our interest and early in the season we persuaded one young, keen farmer and his wife to conduct an experiment. The field on this farm lay on a low hillside facing the front door of the farm and we arranged that every time the farmer or his wife went out at the front door they should glance at the field and place a pebble in one of two hats according as the sheep lay or were eating on the cobalt dressed half or the other. At the end of the Summer we found that the tally showed a ratio of 3 to 1 in favour of the cobalt dressed half of the field. Even if this was a very crude experiment we could not but believe, from the evidence of the well eaten pasture, that for some reason or other the sheep had preferred to eat the cobalt dressed pasture. My colleagues, soil and pasture experts, could find no variation in either soil type or pasture species to account for this. Amongst those whom I took to see this interesting sight was my old teacher and mentor the late Sir Joseph Barcroft and he, though at first sceptical, was eventually convinced that the sheep were selecting the cobalt dressed pasture. In a discussion at the Nutrition Society (*Proceedings of the Nutrition Society*, Vol. 1, Nos. 3 and 4, page 193) he stated, "On a recent visit to some of the pining areas of Ross-shire I was assured that if half a field on the cobalt deficient land was treated with cobalt and the other half left, the sheep would single out the treated land and feed upon it while leaving the other."

As we were more concerned with the practical effects of the observation, rather than it being an interesting phenomenon in animal behaviour, we changed our advice to farmers and suggested that they should topdress their fields in strips—one run of the fertiliser spreader with cobalt plus supers and the next with supers only, until the whole field was topdressed. Again we were informed by a farmer that the strips were obvious to the naked eye owing to the cobalt dressed strips being more eaten down than the others. This was more difficult to believe but a visit to the farm by my colleagues and myself convinced us that the strips could very easily be picked out even at some distance from the field. Again there was no difference in pasture species between one strip and another. The difference in cobalt content between the cobalt dressed pasture and that dressed with supers only would have been approximately 30 parts per hundred million and this, though the difference between adequacy and deficiency as far as the lambs health was concerned, is surely not of an order to have allowed the animals to sense the cobalt itself. It is conceivable that the presence of the extra cobalt in the soil altered the chemical composition of the plant and that the sheep were attracted by

some chemical substance other than cobalt since, if cobalt was acting as an catalyst, the other product might be present in much larger than trace quantities and so influence taste. Chemical analysis has not so far revealed any such product and plant physiologists have been unable to prove that cobalt plays any role in plant physiology or, indeed, that it is essential for plant growth.

The above type of investigation has not been repeated since now we advise farmers to topdress with cobalt the whole area involved. It should be mentioned, however, that we invariably find, if a cobalt-deficient field is divided by a fence and one half is topdressed with superphosphates plus cobalt and the other with superphosphates only and the same number of sheep allowed to graze each half, that the cobalt dressed pasture is eaten down to a much greater extent than that receiving superphosphates only. This effect is not to be confused with that of the free selection experiments discussed above but is due to the action of cobalt on the appetite. In a recent paper (Das and Stewart, *Empire J. exp. Agric.*, **18,** 112) we have shown that lambs on cobalt dressed pasture eat from 50 per cent to 33⅓ per cent more than lambs on cobalt deficient pasture and that this accounts for the variation of length of stem of the pasture on the two sides of the fence.

On many hillsides where it is impossible to topdress the pasture the only practical method of making good the deficiency of cobalt in the pasture is to feed mineral mixtures containing cobalt. The cobalt-rich mineral mixture is placed in hooded troughs, designed so as to preserve the minerals as much as possible from the ravages of inclement weather, and the troughs are placed on the sheep walks or near watering places on the hirsels. Contrary to our expectations we have found the utmost difficulty in persuading cobalt deficient sheep to eat cobalt rich mineral mixtures. In our experiments on major element deficiencies in sheep we have always found that there is a craving by the animal for the particular element missing from its diet and if afforded access to this element it makes full use of the opportunity, indeed, many even stampede the troughs in its attempt to obtain minerals. This does not appear to be the case with cobalt-deficient animals as they appear to be indifferent to cobalt offered them in mixtures or licks. We are at present conducting trials in many different areas of Scotland and it has taken over three years to persuade one Black Face flock to take cobalt-rich minerals readily and this despite the most careful herding of the flock past the troughs at least once daily. We have now just started more intensive work on this subject and by adding flavouring substances, and even scented substances, we are endeavouring to persuade sheep to take these cobalt-rich mineral mixtures as, until aerial manuring becomes a feature of Scottish hill farming, feeding mineral mixtures is the only means of getting minerals into the majority of hill sheep flocks.

We are forced, therefore, by our experience of mineral feeding to come to the conclusion that it was not a craving for cobalt that enabled the sheep in the experiments described above to select the pasture with the additional cobalt and as we can find no botanical or chemical reason for this peculiar selection it remains a fascinating subject for conjecture and discussion as to how the animals obtained singular relish or physiological satisfaction from the cobalt dressed pasture.

The Posture of a Falling Mouse

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Fig. 1

Fig. 2

Fig. 3

The falling mouse adopts a posture which has not yet been fully described or illustrated, and no evidence appears in the literature to help towards the definition of its function. Evidence on both points is presented here.

Figures 1, 2 and 3 are drawings made from flash photographs which show the posture adopted by a mouse in the act of falling. The characteristic features are as follows:

The jaws are partially open. The pinnae of the ears are erect and held at right-angles to the plane of the head. The head itself is invariably held with the snout 10-15° above the horizontal. While the plane of the head with respect to gravity is constant, the rest of the spine may be flexed either dorsally or ventrally in the middle of the back, although the neck is invariably flexed dorsally. The position of the back appears to be determined by the initial impetus accompanying the loss of support. The fore legs are fully extended and protracted, they are held rigid and the fore feet are close together or overlapping. The fore-foot is supinated and the digits are spread apart. The hind legs are also extended and protracted, they are also held rigid, but are wide apart. The hind feet, like the forefeet, are supinated, and the digits spread apart. The tail is frequently in rapid motion and thus in photographs, such as those taken by flash-photography, it is seen in a variety of positions. It appears that the tail is held rigid at the base and may be more or less flexed in any direction towards the tip.

Precipitating Conditions

The posture is fully developed by the normal mouse within a quarter of a second of loss of support; although it has not been possible to obtain photographs within a shorter interval, observation of the mouse suggests that it develops much more rapidly. This is also suggested by the fact that it can be elicited if a mouse is held by the tip of the tail and the hand jerked downwards. Some strains of laboratory mice have been found to contain a proportion of animals which when stimulated by this procedure, developed a convulsion which perpetuated this posture for several seconds, (frequently as long as five seconds, and in a few instances twice as long as this). Throughout the convulsion the mouse was tense and trembling vigorously. Two strains have been bred in this laboratory, H.C. 1—a brown agouti obtained from Dr. Hagedoorn, which contained 70-80% incidence of this type of susceptible mouse; and another H.C. 2 which was bred from an albino stock, and which after 6 or 7 generations of selective breeding, contained 25% incidence. Some drugs, notably Picrotoxin and to a less marked extent Leptazol (Pentamethylenetetrazol) evoke this posture in the early stages of a convulsion produced by clonic convulsive doses.

Neurophysiological Mechanism

Lyon (1951) has examined some postural components of this behaviour, in normal and pallid mice, some of which possess abnormalities in their postural reflexes, and has investigated the inheritance and anatomical basis of these defects. Testing the response to position change by holding the mouse up by its tail, she found

that in normal young mice the spine is flexed dorsally and head is raised, and also that the fore limbs are protracted and extended. This is the posutre adopted by the adult mouse held in the same position, but only after the hand has been jerked downwards. The pallid mouse did not develop this posture on being held by the tail, and by the 3rd or 4th week the normal mouse does not show this tendency to such a marked degree. The interest of her anatomical findings is, that the absence of this response in the young pallid mouse is due to the bilateral absence of otoliths from the maculae of the utriculus and usually also the sacculus. She has suggested that the maculae without otoliths emit a resting discharge; and if so this discharge could also be brought about in the adult animal by the absence of gravitational force during a fall. It is probable, therefore, that the response of the otoliths to the absence of gravitational pull during a fall is one important component of the stimuli evoking the falling posture.

Functional Role in Behaviour

It is widely known that mice can fall considerable distances without injury, and on the other hand it is also known that many animals adopt characteristic postures while falling, which are generally regarded as constituting a suitable landing posture. In order to find out whether this posture protected the mouse against the damage of impact at the end of a fall, five male mice weighing 25-32 gms. were injected with 2 mgm. of seconal to bring about complete muscular relaxation and anaesthetisation. The depth of anaesthesia was judged by the loss of the righting reflex and of the corneal reflex. Animals which had reached this level of central nervous depression were dropped 10 feet on to a hard surface by simple withdrawl of support. For comparison five normal mice were dropped; and on landing the normal mice moved away normally. One hour later before the anaesthetised mice had recovered from the anaesthetic, both groups were killed and examined for haemorrhage. The results are presented in the Table.

Table. Haemorrhagic Lesions Following 10-foot Fall.

Normal Mice.	Anaesthetized Mice.
1. One small lesion in fat body of the left pelvis.	1. a. Blood clots throughout peritoneal cavity. b. Haemorrhagic lesion in cleidomastoid muscle close to posterior border of skull. Animal died 20 mins. after fall.
2. No lesion	2. a. Small haemorrhagic lesion in fat of neck. b. Large haemorrhagic lesion in cleidomastoid muscle close to the posterior border of the skull. c. Large haemorrhagic lesion in sartorious muscle close to the hip joint.
3. No lesion	3. a. Small haemorrhagic lesion in mesentery of gut. b. Two small haemorrhagic lesions in vessels covering lumbar region of spine. c. Small haemorrhagic lesion in peritoneal fat.
4. No lesion	4. Blood clots on gut mesentery and in peritoneal cavity.
5. No lesion	5. a. Blood clots on gut mesentery and in peritoneal cavity. b. Small haemorrhages in sartorious muscle close to hip joint.
Total lesions: 1 No. of animals affected: 1	Total lesions: 11. No. of animals affected: 5.

The table showed that whereas only one of the normal mice received slight damage, lesions occurred in all the anaesthetised animals and were extensive, consisting mainly of internal haemorrhages, the most severe of which occurred in the mesenteries of the gut. Since all these haemorrhages were localised at restricted points and did not occur diffusely, it is likely that they are produced by nodes in concussion waves.

Summary

The posture of the falling mouse has been described and illustrated. Some evidence relating to precipitating conditions has been brought forward and evidence that it protects the mouse against the effects of concussion on landing is presented.

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Correspondence

The Stridulation Behaviour of the Domestic Cricket

Recent work by Busnel & Chavasse (1950), Evans (1952) and Broughton (1952) on stridulation in Orthoptera is almost entirely confined to recording and analysis of stridulation, and no attempt at a study of the associated behaviour has been made.

Some controversy is apparent over the best method of recording and analysis; tape recorders, oscilloscopes and disc recordings have all been used. To get over the difficulty in this work on the stridulation of *Gryllulus domesticus* L. I have used both tape recording and direct oscillographic analysis; work on the frequency analysis was done with two audio spectrometers, one checking the other.

The adult male domestic cricket has two distinct songs; the first may be termed the "normal song" and is made with the tegmina held up from the dorsal surface of the abdomen at about 45°. It consists of an irregular series of chirrups and each chirrup comprises from one to twelve pulses of sound. These pulses are made at a regular frequency of about 20 cycles per second. Each pulse consists of a number of sound waves of a complex nature with an average fundamental frequency of 3,500 cycles per second.

This fundamental frequency can vary with different insects over a range of about 500 cycles on either side of the average, but the pulse frequency appears to remain constant at about 20 cycles per second.

The second type of song may appropriately be called the "courtship song." It sounds like a long low trill and while making it the male flattens its body against the ground and rocks from side to side on its legs with antennae gently waving in front. The tegmina are held nearly flat on the back during this song. The fundamental frequency of the "courtship song" is about 2,000 cycles per second, again with a variation of about 300 cycles on either side of this average for different individuals.

No observable reactions of any sort were produced when playing back recorded stridulation to male crickets.

Normal adult females were stimulated by recorded or relayed stridulation to a positive reaction in the form of short bursts of locomotor activity taking them distances of up to eighteen inches from their starting point; this was observed in 58% of cases in 150 trials. Positive response was reduced to 27% if the tympanal organs were destroyed by electric needle and to 10% if the tympanal organs were destroyed and anal cerci covered with vaseline.

Positive reaction of female crickets to the "courtship song" consists of inhibition of locomotor activity and general passiveness of behaviour; this reaction facilitates mating by allowing the male to slide his abdomen under the female (irrespective of orientation of the latter) and attach the genitalia. With normal adult females 60% positive reactions in 150 trials occurred, which was reduced to 37% when tympanal organs were destroyed, and to 15% when tympanal organs were destroyed and anal cerci covered with vaseline.

The results are interesting in the light of the work of Pumphrey and Rawdon-Smith (1936 a, b, c, 1939) on insect hearing; they showed that it is doubtful if insect tympanal organs are frequency discriminators, but are probably sensitive to modulation. Furthermore, they showed the sensillae of the anal cerci of crickets were sensitive to sounds particularly in the low frequency range of about 40-50 cycles per second.

This modulation may be the important quality of insect noises and to test this the foregoing experiments were repeated, using first normal recorded stridulation and then recorded stridulation from which the fundamental frequency had been cut by means of an electrical filter.

In these experiments, using normal adult females only, 54% positive reaction in 150 trials were obtained with ordinary "normal song" and 40% to "normal" song less fundamental frequency. Similarly in reactions to the "courtship song" 58% positive reaction in 150 cases were obtained with the "normal" recording and 52% with the filtered recording.

The work of Roeder (1948) and Cook (1951) shows that in some Orthoptera a caudal neuromuscular system exists which helps to explain the kinetic reaction shown by adult females in response to the "normal song" of the male.

A tentative hypothesis may be erected explaining stridulation behaviour. In an aggregation of crickets, at any given moment some males will be performing the "normal" and

others the "courtship" song. Females hearing the "normal" song will be stimulated to locomotor activity and this will increase the chances of their coming close to a male singing the "courtship" song, with increased possibilities of mating.

The stridulation would thus have survival value in bringing the sexes together for mating and in reducing the time between this encounter and subsequent copulation. This view is supported by Khalifa (1950).

Although this hypothesis explains the observed facts of the stridulation behaviour of crickets, it is presented tentatively, since various basic assumptions, such as the sensitivity and operation of the caudal-thoracic neuro-muscular system remain to be tested. Work on these further aspects is now proceeding and fuller details of the present work will be published elsewhere as soon as possible.

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Book Review

Parental Care and its Evolution in Birds. By KENDEIGH, S. C., University of Illinois Press (1952). Pp. 356. Paper $4.00. Cloth $5.00.

The extensive literature on the parental care of birds has hitherto never been adequately summarised. The scattered and often fragmentary nature of the material have made it virtually inaccessible to the ornithologist, so that new data could not be placed against their proper biological background. This is no longer the case: Dr. Kendeigh has now welded these heterogeneous observations into a coherent whole which provides valuable information for students of evolution, ecology and behaviour.

His success is largely due to the mass of detailed data on *Troglodytes aedon*, gathered principally by the author himself, which serves as a central core round which the less detailed data on other species are built. His records extend over many years, and he has made extensive use of mechanical recording techniques. The results demonstrate clearly the value of intensive observations on one aspect of the life history of a species. Two points, however, must be mentioned. First, his analysis of behaviour into periods of "attentiveness" and "inattentiveness" rests on the assumption that there are only "two basic drives involved, that of self-maintenance or existence and that of reproduction." Periods of attentiveness often (though not always) refer to periods which include several different types of reproductive behaviour. The data would have been of much greater value if these concepts had been analysed in greater detail. Second, some of the conclusions could have been stated more precisely if proper use had been made of statistical techniques.

This section on *Troglodytes aedon* is followed by comparable but less complete data for nineteen other species, and then by an extensive review of the literature on parental care in all avian groups arranged in systematic order.

The main value of the book lies in the facts which it presents and summarises: only some 34 of the 356 pages are devoted to discussion. The pages on the evolution of parental care, with which the book is concluded, indicate the complexity of the factors involved and demonstrate that, in a discussion of adaptation, each aspect of the physiology and behaviour of a species must be considered as part of an integrated whole.

Dr. Kendeigh's book provides a new starting point in the study of parental behaviour, and will be a reference book for ornithologists for many years to come.

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